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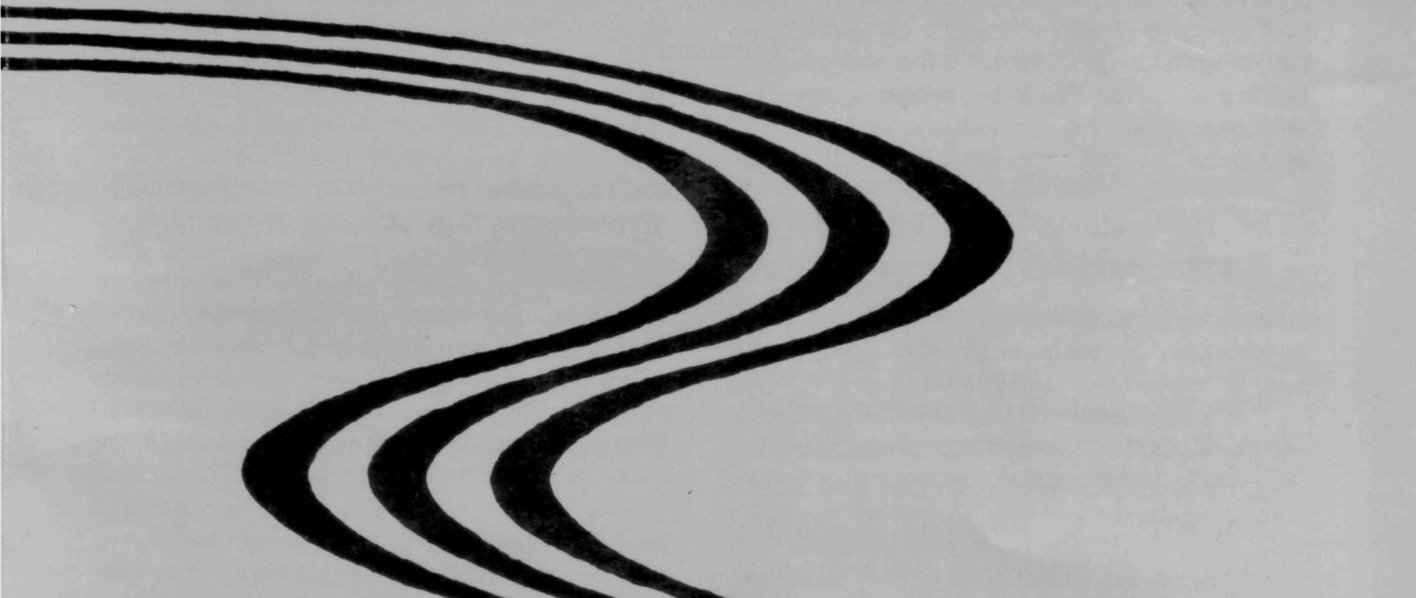

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MECHANISMS UNDERLYING STABILITY IN COMMUNITIES OF AQUATIC MICROORGANISMS: THE ROLE OF CILIATE PREDATION ON COMPETING ALGAE AND BACTERIA

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ABSTRACT. Competition for food resources between algae and bacteria and the effects of ciliates on outcome of this competition were studied using experimental and mathematical modelling methods. The results of these studies allow to propose two new mechanisms providing stability in communities of aquatic microorganisms and the role of predation in its sustaining. One of them is the regeneration of limiting substrates (nutrients) by the predator, which may improve conditions for the inferior competitor. The other one is the transforming of limiting substrate by the predator into a form more appropriate for the prey. In natural waters where microbiological processes are limited by nutrient concentrations the proposed mechanisms of stabilization may be important in structuring the communities of aquatic microorganisms.

Key words: aquatic microorganisms, competition, predation, community, stability mechanisms, nutrient recycling.

Introduction

Theoretical studies of community and ecosystem stability are quite numerous, but applicability of the results of many such studies is problematic due to the lack of experimental support. The definition of stability itself is far from being universely accepted; here, following Svirezhev (1987), stability is understood as ability of a community to retain its species composition in a varying environment. As far as experimenting with natural ecosystems is impossible and/or undesirable, a necessity exists to perform experiments with simple laboratory communities. A great experimental work has been done with such communities and many mechanisms of stability have been proposed. There is large literature on the role of predation in stabilizing community structure. The mechanism described most often is a suppression by a predator of the superior competitor among preys. The predators on bacteria and algae have been considered as the main agents of nutrient recycling, but a possible relationship between the nutrient regeneration by the predators and community stabilization has not been identified. In my previous works (Umorin 1974, 1976, 1992a, b) nutrient regeneration by predators on bacteria and algae (ciliates and flagellates) has been shown to stimulate these prey and provide for their better growth and activity. One the basis of these data a hypothesis may be formulated that predators may stabilize a system of competing prey by mechanisms other than suppression of the superior competitor, e.g. by making the competition for a common food resource less acute through regeneration of this resource. The objective of this work is to test this hypothesis in experiments with algae and bacteria as prey organisms and ciliates as predators.

Methods

The studies were performed using continuous flow-through cultures of algae and bacteria as prey organisms competing for nutrients, and ciliates as bacterial grazers (predators).

One group of experiments (Table 1) was conducted with a community consisting of a mixed culture of bacteria (obtained by inoculating nutrient medium with pond water), an alga *Scenedesmus quadricauda* Breb., and a ciliate *Cyclidium glaucoma* O.F.Müller under the conditions of varying supply of mineral nitrogen and glucose as a source of organic carbon. Variations in the concentrations of nitrogen and organic carbon were planned as to provide different degree and character of prey growth limitation in order to obtain presumably different community responses, thus making it easier to ascertain the predator's role in the limiting substrate turnover and community stabilization.

The second group of experiments was designed to include a disturbance agent which would lead to inhibition of some of the prey and finally to its extinction, i.e. collapse of the community, since under this condition it is easier to reveal the stabilizing role of a predator. Additions of potassium chlorate ($KClO_3$) in concentrations slightly toxic to algae and bacteria and indifferent to ciliates (as was previously established in short-term tests), were used as a disturbance factor. Chlorate is quite common anthropogenous pollutant; it was chosen because the Institute, at which the author works, has long dealt with strong oxidizing agents (chlorate among them) and gained some knowledge of their effects on aquatic organisms. The experiments of this group were performed with the same cultures of bacteria and algae as in group 1, and a ciliate *Paramecium caudatum* Ehrenb.

A continuous culture unit (LKB company, Sweden), was used operated as a chemostat at a dilution rate of 0.005/h; in the second group an additional set of experiments was performed according to the same scheme (Table 2), but with a dilution rate of 0.01/h. In the 1st group of experiments the nutrient medium was Chu-10 modified in respect to nitrate nitrogen and glucose contents, as shown in Table 1 in the column «Medium». In the 2nd group nitrogen concentration was reduced to 1.0 mgN/L in all the treatments to make it a limiting factor of bacterial and algal growth.

The medium was supplied by a two-channel peristaltic pump to two parallel two-litre reactors. One of the reactors was inoculated with bacteria, algae and ciliates; the other one contained only algae and bacteria and served as control. Two runs were performed in sequence, hence the data were collected as a set of two replicates in time. The algal and ciliate's numbers were obtained by means of counting samples in chambers; dead and living algae were distinguished by the bright red fluorescence of the living ones in the ultraviolet light under a microscope. Bacterial number was determined by direct counts on erythrosine stained membrane filters. The organisms abundance thus obtained was converted into dry organic matter concentration, taking into account dimensions of the organisms and assuming their dry weight was 10% of their wet weight, wet biomass density being one.

Mathematical modelling

Another way to test a hypothesis is to formulate it in the form of a mathematical model and analyze results of computer simulation of the model. Thus, modelling provides an answer to the question: to what results will certain assumptions about the simulated system inevitably lead? Here, we are to be sure that the model is realistic, i.e. it describes the real system (behavior of the microbial community in our case) adequately. For this purpose the results of actual experimenting with the real system and results of computer simulation of the model should be compared. If both the real system and the model behave similarly, i.e. respond in the same manner (at least qualitatively) to the same disturbances, than the model may be considered adequate to the real system. Therefore, its our belief that in solution of scientific problems experimenting with real systems and mathematical modeling should ac-

Table 1. Scheme of 1st group of experiments

Series	Medium	No.	Treatment	Organisms used
I	N = 1.5 mg/L without glucose	1	Control	Algae + Bacteria
		2	Experim.	Algae + Bacteria + Ciliates
II	N = 1.5 mg/L glucose 10 mg/L	3	Control	Algae + Bacteria
		4	Experim.	Algae + Bacteria + Ciliates
III	N = 0.5 mg/L glucose 10 mg/L	5	Control	Algae + Bacteria
		6	Experim.	Algae + Bacteria + Ciliates

Table 2. Scheme of 2nd group of experiments

Series	Medium	No.	Treatment	Organisms used
I	without chlorate	1	Control	Algae + Bacteria
		2	Experim.	Algae + Bacteria + Ciliates
II	chlorate 450 mg/L	3	Control	Algae + Bacteria
		4	Experim.	Algae + Bacteria + Ciliates

company and supplement each other. At the next stage of investigations the adequate model acquires an independent (on the real system) status, and may be used as a substitute for the real system. Computer simulation experiments may be performed with the model to gain information about the real object. That was the reasoning in this work behind the use of mathematical models.

Mathematical models were developed for the both groups of experiments to analyze the relationship among algae, bacteria and ciliates. The models require a separate special consideration and are dealt with in detail elsewhere in our publications (Umorin 1991, 1992a). It was assumed that the rate of biomass change results from the changes in the rate of their growth, mortality, grazing and washout from the reactor. The growth rates of the organisms are functions of the food substrate concentrations. This relationship follows Michaelis-Menten kinetics, which is generally accepted. It is also assumed, that reduced forms of nitrogen are preferred by algae and bacteria over the oxidized form (nitrate), supplied with the medium. In general, the equations for the living components are Verhulst-Pearl equations, where the death rates of the organisms are proportional to the square of their biomass, which cannot exceed a certain value called the carrying capacity for the given medium.

For computer simulation of the experimental systems the values of the model parameters should be known. To determine the main parameters (specific growth rates and half-saturation constants) additional short-term experiments with batch cultures of algae and bacteria were performed using different concentrations of two forms of nitrogen, and also with and without chlorate. The remaining parameters were taken from our own previous studies (Umorin 1980, 1983) and from the published data of other authors (Curds 1974; Buhr and Miller 1983; Rogers and De Pinto 1983).

Results

Experiments with flow-through and batch cultures

On the average on the 20th day steady states were established in all the experiments. In the 1st group (Table 3) algae and bacteria developed quite well in the series I, and a stable system of producers and decomposers of organic matter was established in the control. Competition for nitrogen here was not of primary importance, since its sufficient amount was supplied with the inflowing medium. Addition of ciliates did not change principally relationship between algae and bacteria; the latter were just reduced in biomass due to grazing.

Addition of glucose in the series II lead to a greater development of bacteria and lesser development of algae in the control. In this series competition for nitrogen became more intensive, as a greater amount of it was required for the bacterial growth stimulated by glucose. Thus, a tendency towards extinction of an inferior competitor (algae) was observed as a result of the intensified competition. Presence of ciliates in this series caused a greater reduction in bacteria and a greater increase in algae as compared with series I, counterbalancing the trend towards competitive exclusion of algae.

The most dramatic effect of the ciliate presence was observed in series III with low nitrogen and high glucose supply. Here competition for

Table 3. Organism biomasses (mg/L) at steady state. 1st group of experiments (means of 2 replicates, CV=23%) Obs. — experimental data, Mod. — computer simulation data

Series	№	Treatment		Algae	Bacteria	Ciliates
I	1	control	Obs.	11.4	1.7	—
			Mod.	12.1	1.9	—
	2	experim.	Obs.	12.2	0.8	0.3
			Mod.	12.7	0.5	0.5
II	3	control	Obs.	7.7	6.1	—
			Mod.	7.9	5.8	—
	4	experim.	Obs.	11.1	0.7	1.2
			Mod.	11.9	0.6	1.8
III	5	control	Obs.	0.0	3.8	—
			Mod.	0.0	4.7	—
	6	experim.	Obs.	2.5	0.6	0.8
			Mod.	2.7	0.4	1.0

nitrogen was a factor of utmost importance in determining species composition of the community involved. Algae were completely exterminated in the control, being inferior competitors to bacteria for nutrients. Ciliates imparted stability to the system of two competing prey organisms, making their coexistence possible.

In studies with chlorates the short-term experiments conducted for estimation of the growth parameters of algae and bacteria are of interest by themselves. Their results are presented in Table 4. Remarkably, that half-saturation constants in a medium with reduced form of nitrogen (ammonium) were significantly lower ($p < 0.01$) than with nitrate, independently on chlorate presence. This means, that on equal concentrations of nitrogen algae and bacteria grow faster in media with ammonium nitrogen; the former react more conspicuously to a change of the nitrogen form.

The presence of chlorate caused a sharp decrease in the actual growth rate of organisms, especially algae, cultured in the medium containing nitrate as the only nitrogen source. The half-saturation constant on nitrate in algae became an order of magnitude higher and in bacteria four times as great as on ammonium, which is indicative of lower affinity for nitrate than for ammonium in this organisms. It is important to note, that the maximum specific growth rates in both algae and bacteria were not affected by chlorate; this means that the decrease in the actual growth rate occurred according to the principle of competitive inhibition: two substrates, chlorate and nitrate, competed for the same enzyme, namely nitrate reductase. This competition has been described in the literature (Balch 1985).

The results of the 2nd group of experiments with flow-through cultures are shown in Tables 5 and 6. In these tables symbol «Obs.» stands for the observed experimental data, «Mod1» for results of «normal» modeling with an assumption that nitrogen excreted by ciliates is in a reduced form (parameters for simulation were taken from Table 4 for ammonium). «Mod2» designates results of modeling with an assumption, that nitrogen excreted by ciliates is consumed by algae and bacteria at the same rate as nitrate nitrogen.

As seen from Tables 5 and 6 algae and bacteria could coexist at both dilution rates without ciliates' presence, if no disturbance agent (chlorate) was involved (series I). Ciliates here simply decreased the biomass of bacteria and increased that of algae, just as in series I and II in the 1st group of the experiments. But under the stress of disturbance (series II, with chlorate)

Table 4. Maximum specific growth rates (μ, h) and half-saturation contants for nitrogen source (K, mg N/L)

Treatment and Nitrogen source		Algae		Bacteria	
		μ	K	μ	K
Without chlorate	nitrate	0.087	0.093	0.41	0.022
	ammonium	0.098	0.021	0.38	0.012
With chlorate	nitrate	0.103	0.890	0.44	0.094
	ammonium	0.091	0.027	0.37	0.017

Table 5. Organism biomasses (mg/L) at the steady state in the 2nd group of experiments. Dilution rate = 0.005/h (Means of 2 replicates, CV=19%)

Ser.	No.	Treatment		Bacteria	Algae		Ciliates	Total dissolved N
					living	dead		
I	1	control	Obs.	4.60	0.61	0.08	—	—
			Mod1	6.01	0.38	0.00	—	0.003
	2	experim.	Obs.	1.23	3.04	1.86	0.9	—
			Mod1	0.48	3.65	3.90	1.1	0.017
			Mod2	0.47	3.20	2.25	1.4	0.060
II	3	control	Obs.	4.31	0.00	0.00	—	—
			Mod1	5.20	0.00	0.00	—	0.003
	4	experim.	Obs.	2.51	3.40	5.72	1.1	—
			Mod1	2.12	4.92	10.43	1.8	0.157
			Mod2	0.71	0.60	0.06	1.4	0.250

algae and bacteria could not coexist, and washout of algae from the reactor occurred in the absence of ciliates. Presence of the latter prevented exclusion of algae, and led to establishment of a stable community of bacteria, algae, and ciliates.

Computer simulations

The mathematical models show a good correspondence to the observed experimental data in the sense that the models behave in the same way as experimental systems, i.e. respond similarly to the same factors. This conclusion can be inferred from comparison of the experimental and computer simulation data in Tables 3, 5, and 6. Therefore, the models were considered adequate for use in analysis of the experimental results and for computer experiments to get additional information about the modelled communities. It was of interest to see if stabilization of the algae-bacteria system had been caused by suppression of the superior competitor (bacteria) by the predator (ciliates), as may be assumed from a number of publications (Abrosov and Kovrov 1980; Parrish and Saila 1970). To test this assumption the values of organic matter production by algae and destruction by bacteria were calculated with a help of the model developed to simulate the 1st group of experiments (Table 7).

As seen from table 7, the ciliates enhanced production of organic matter by algae in all the treatments, at the same time they stimulated destruction of organic matter by bacteria. The only exception is the series II, where the ciliates really suppressed the bacteria, i.e., diminished their abundance and activity simultaneously. But the stabilization effect was observed in series III; so, inhibition of bacteria might not be the cause of the observed coexistence of algae and bacteria in these experiments.

Many computer experiments were performed with the model to determine the biomasses of organisms at steady states under various conditions of nitrogen and organic carbon supply and using different organism growth parameters and different dilution rates. The goal of such experimenting was to find conditions under which the maximum stimulation of algae and maximum inhibition of bacteria would occur. At the same time the values of nitrogen regeneration by ciliates were estimated. In all the cases the maximum stimulation of algae occurred at low nutrient levels and high organic matter content; just the conditions under which the maximum relative regeneration rates were also found. The

Table 6. Organism biomasses (mg/L) at steady state in the 2nd group of experiments. Dilution rate = 0.010/h (Means of 2 replicates, CV=17%)

Ser.	No.	Treatment		Bacteria	Algae		Ciliates	Total dissolved N
					living	dead		
I	1	control	Obs.	5.10	0.46	0.15	—	—
			Mod1	6.30	0.22	0.12	—	0.004
	2	experim.	Obs.	2.80	3.79	4.22	1.2	—
			Mod1	2.14	4.11	7.43	1.7	0.221
			Mod2	2.61	2.82	2.04	1.7	0.508
II	3	control	Obs.	5.06	0.00	0.00	—	—
			Mod1	5.78	0.00	0.00	—	0.004
	4	experim.	Obs.	2.54	3.48	5.16	1.4	—
			Mod1	2.20	3.92	6.30	1.6	0.610
			Mod2	2.87	0.07	0.09	1.7	0.660

Table 7. Production and destruction of organic matter (mg/L per day) in the 1st group of experiments at the steady state.

Series	No.	Treatment	Production	Destruction
I	1	Control	1.70	0.38
	2	Experim.	1.87	1.18
II	3	Control	1.13	1.53
	4	Experim.	1.73	1.32
III	5	Control	0.00	0.96
	6	Experim.	0.38	2.74

maximum stimulation never coincided with the maximum inhibition of bacteria. This leads to a conclusion that recycling of nutrients without suppression of a superior competitor may be one of the mechanisms by which a predator imparts stability to otherwise unstable communities.

Concerning analysis of the second group of experiments it may be stated that in the medium without chlorate in the absence of ciliates algae and bacteria coexisted but very close to the margin of stability range, because of the low algae biomass. Computer simulations showed that with an increase in the dilution rate (imitation of natural elimination) washout of algae from the reactor would occur. In the presence of ciliates the algae biomass increased by an order of magnitude, and the bacterial one dropped. This was due to a competition between algae and bacteria which the ciliates made less intense by grazing on the superior competitor, i.e., bacteria (ciliates *P.caudatum* do not feed on algae *S. quadricauda*).

The character of relations between algae and bacteria became more acute in the case of chlorate addition (series II). The latter reduced the algal capacity of competition by not allowing them to consume nitrogen at a rate sufficient to compensate for the washout through the mechanism mentioned above. In the presence of ciliates a stable community «algae - bacteria - protozoa» was established, capable of existing under the influence of chlorate.

Use of the model allows to understand the mechanism by which the community was stabilized. Results of simulations showed dissolved nitrogen concentration to be one or two orders of magnitude higher in the presence of ciliates, which allowed the algae to maintain high growth rate and avoid elimination. Thus, another mechanism underlying stability (already revealed in the 1st group of experiments) manifested itself here: regeneration of the limiting substrate and acceleration of its turnover by a predator.

However, as the results of simulations according to «Mod2» mode showed, this mechanism alone is not sufficient to secure a stable existence of the community under deteriorating conditions. At a dilution rate 0.005/h it was sufficient (Table 5), but at 0.010/h it was not (Table 6, biomass of the living algae of 0.07 is almost their elimination). Simulations according to the mode «Mod1» proved one more mechanism of stabilization was at work: liberation of the limiting substrate by a predator in a form more preferable by the prey. This is also confirmed by the fact that the simulated dissolved nitrogen concentrations in rows «Mod1» are even lower than in rows «Mod2» due to increased consumption by algae and bacteria.

Discussion

The results of experimental and mathematical modeling studies presented here allow to propose two new mechanisms underlying stability in communities of aquatic microorganisms. They consider the role of predation in stabilizing the community of prey competing for a common food source. The importance of protozoan predation on bacteria for nutrient recycling has been shown in experimental studies (Umorin 1974, 1976) Later, many potential predators on bacteria and algae have been acknowledged as the main agents of nutrient recycling in both fresh and sea water (Porter et al. 1985), but a possible relationship between the nutrient regeneration by the predators and community stabilization has not been identified. One of the proposed mechanisms consists in regeneration of limiting substrates (nutrients) by the predator, which may improve conditions for the inferior competitor. The other one is actually conversion of the limiting substrate by the predator into a form more appropriate for the prey.

Many mechanisms underlying the stability of simple biotic communities have so far been proposed. One of them, developed theoretically (MacArhtur and Levins 1967, Abrosov and Kovrov 1980), requires that, for a community of competing organisms to be stable, each organism should be limited by a separate individual substrate. Therefore, the number of substrates should not be less than the number of organisms. The experimental evidence concerning this mechanism is conflicting. In experiments with three species of ciliates Hairston (Hairston et al. 1968) found, that homeostasis of the system increased a little, if diversity at the bacterial level also increased. In similar experimental work, Luckinbill (1979) observed that when the prey organisms were represented by many species, the predators quickly attained high numbers and finally exterminated all the prey.

Many publications touch on the role of predation in stabilizing community structure, and there are many disagreements over this point (e.g. Thorp 1986). It has been shown both experimentally and theoretically (Paine 1966, Parrish and Saila 1970, Fuji 1977), that predators may impart stability to otherwise unstable systems of competing prey by suppressing a prey, which is superior in competition. In association with predation some other mechanisms of simple community stability have been suggested. These are patchiness of the environment and presence of refuges for the prey (Holt 1987). In the author's previous work (Umorin 1992b) another mechanism of stabilizing has been formulated, based on the fact, that in real ecosystems organisms do not belong strictly to one trophic level, because they usually feed on a variety of resources. Earlier (Umorin 1981) this mechanism was shown to stabilize a system of two competing algae, one of which was an inferior competitor for organic substrates but had a greater rate of photosynthesis. Similar approaches have been developed by Petraitis (1989) for representation of the ecological niche breadth and overlap, where he has shown that the rates of resource consumption are very important in determining the result of competition.

In the theoretical works mentioned above the mechanisms of stabilizing proposed here were not identified, since these works considered an abstract limiting substrate without taking into account its real nature and the fact, that it may be regenerated and transformed by the predator. A simple suppression of the superior competitor may, in our view, serve as a mechanism of stabilization only under favorable growth conditions when the predator has «nothing to improve». In natural waters the microbiological processes are, as a rule, limited by nutrient concentrations, and the stability mechanisms proposed here are, probably, important in structuring the communities of aquatic microorganisms.

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Механизмы устойчивости сообществ водных микроорганизмов: влияние хищника (инфузорий) на конкуренцию водорослей и бактерий

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РЕЗЮМЕ. Экспериментальным методом с применением математического моделирования изучена конкуренция за пищевые ресурсы между водорослями и бактериями и влияние инфузорий на исход этой конкуренции. Результаты исследования позволяют предложить два новых механизма устойчивости сообществ водных микроорганизмов, касающиеся роли хищничества. Один из них заключается в регенерации пищевых субстратов (биогенов) хищником, что может улучшить жизненные условия для более слабого конкурента. Второй механизм — это превращение лимитирующего субстрата хищником в более приемлемую для жертвы форму. В естественных водоемах, где микробиологические процессы лимитируются концентрацией биогенов, предложенные механизмы устойчивости могут иметь важное значение в формировании структуры сообществ водных микроорганизмов.

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